

# Effects of long-term consumer manipulations on invasion in oak savanna communities

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**Abstract.** Consumer–plant interactions can alter the outcome of biological invasions when native and exotic plants differ systematically in their resistance to and/or tolerance of consumer impacts. Given evidence for indirect interactions and shifts in plant communities from the few existing long-term studies, it is clear that long-term studies are a critical component for understanding the role of consumers in plant invasions. Moreover, studies of the role of consumers in mediating invasions have focused on the effects of exotic consumers, while the effects of native consumers on invasion have received little attention. Here we examine the long-term impact of a largely native vertebrate consumer community on native and exotic understory plants and recruitment of native oaks in a California oak savanna. We sampled plant community composition, oak recruitment, and soils inside and outside of 10 exclosures (mean area = 1000 m<sup>2</sup>) that had been in place for an average of 32 years. Plots with consumers present had 41% more exotic species, 31% higher cover of exotic species, and 33% lower richness of native herbaceous perennials, suggesting that native consumers may play an important role in mediating invasion in this system. The presence of oak canopies had a strong impact on the plant community independent of consumer effects, with greater recruitment of oaks, higher cover of native shrubs, and lower cover of exotic species cover under oak canopies. The concordant variation of native tree canopy and native woody plants suggests that adult oaks provide a refuge for their seedlings and other native woody plants. Thus, the widespread loss of native oaks has likely increased exotic invasion into an important refuge for native species in the California oak savanna ecosystem.

*Key words:* consumer exclosure; grassland; herbivory; mutualism; positive interactions.

## INTRODUCTION

Consumers can have profound impacts in ecological systems: consumers alter the dynamics of plant populations (Louda et al. 1990), change the composition of plant communities (Hulme 1996, Howe and Brown 1999, Keane and Crawley 2002, Howe and Lane 2004), alter nutrient flux in ecosystems (Bakker et al. 2004, Cebrian 2004, Lartigue and Lartigue 2004), and shape plant evolution (Strauss and Agrawal 1999). Given consumer-specific impacts (Hulme 1994, 1996, Howe and Brown 1999, Howe et al. 2006) and the potential for interactions among consumers capable of changing total consumer impact (Orrock et al. 2003, Borer et al. 2007, Pringle et al. 2007), ascertaining consumer impact is best accomplished using studies that manipulate more than one consumer guild. Moreover, because dynamics of plant communities may require many seasons to become evident, long-term studies are the most effective way to understand the ultimate effect of consumers on plant communities (Bakker and Moore 2007). The insight possible from long-term studies that manipulate con-

sumer guilds is evident from classic work in desert (Brown and Heske 1990) and prairie plant communities (Howe and Lane 2004, Howe et al. 2006). Despite the need for such studies, most plant–consumer studies manipulate only one or a few consumers over short time scales (Gruner et al. 2008).

Consumer–plant interactions can alter the outcome of biological invasions when natives and exotics differ systematically in their resistance to and/or tolerance of consumer impacts (Chesson 2000, Maron and Vila 2001, Keane and Crawley 2002). Studies of the role of consumers in mediating invasions have primarily focused on the effects of exotic consumers on native and exotic species. These studies of exotic consumers fall in two broad groups. First are studies that test whether exotic species have fewer natural enemies in their invasive than in their native range, the enemy-release hypothesis (Keane and Crawley 2002, Torchin and Mitchell 2004, Mitchell et al. 2006). Second are studies that show that, in general, exotic consumers have stronger effects on native than exotic species (Parker et al. 2006). In contrast, the effects of native consumers on invasion have received less attention; existing studies show that native consumers may either facilitate (Schiffman 1994, Seabloom and Richards 2003, Orrock et al.

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TABLE 1. Location and basic specifications of exclosures at Hastings Natural History Reservation, California, USA.

Exclosure name	Area (m <sup>2</sup> )	Location	UTM northing	UTM easting	Year built	Large vertebrate access	Climber access	Burrower access	Citation or PI†
2GRIFFA	2000	School Hill	629738	4027224	1965	no	yes	yes	Griffin (1971)
3GRIFFA	2000	School Hill	629666	4027004	1965	no	yes	yes	Griffin (1971)
5GRIFFA	500	Red Hill	629975	4028209	1965	no	yes	yes	Griffin (1971)
6MUICK	45	North Field	629818	4027937	1987	no	no	no	Muick (1991)
7MUICK	45	Robertson Saddle	630299	4027435	1987	no	no	no	Muick (1991)
8MUICK	45	Martin Road	630264	4026864	1987	no	no	no	Muick (1991)
11GRIFFC	25	Pierson 1	629235	4027411	1982	yes	yes	no	Stromberg and Griffin (1996)
12BOUC	60	Well	629605	4027668	1980	no	yes	no	Boucher (1985)
13MENK	1500	Arnold Road	628744	4026416	1985	no	yes	yes	J. W. Menke
14KNOP	6500	Arnold Road	628716	4026359	1992	no	yes	yes	Knops et al. (1996)

Note: UTM coordinates are for Zone 10S.

† PI, primary investigator.

2008a, b) or suppress exotic invasion (Parker et al. 2006).

Here we examine the long-term impact of vertebrate consumers on the cover and richness of native and exotic understory plants and recruitment of native oaks in an oak savanna community in central California. As of 1991, there were 32 endangered, threatened, or rare species and over 1500 plants, insects, and vertebrates associated with California oak communities (Pavlik 2000). The oak savanna community is of great conservation concern primarily due to an apparent lack of oak regeneration. Lack of regeneration may be due to increased grazing pressure, removal of oak herbivore predators, trampling by livestock, competition with other species, or novel pathogens (e.g., sudden oak death; Rizzo et al. 2002, Rizzo and Garbelotto 2003). Although native mammalian consumers are ubiquitous in California grasslands and savannas (Schiffman 2007), and can have large impacts on oaks and native herbaceous plant communities (Batzli and Pitelka 1970, Borchert and Jain 1978, Rice 1987, Borchert et al. 1989, Seabloom and Richards 2003, Seabloom et al. 2005), there is no comprehensive, long-term experimental study of their impacts on grassland invasion and oak dynamics.

We examined oak recruitment and the composition of understory vegetation inside and outside 10 exclosures established over the past 40 years by a variety of investigators working on a research reserve in central California. By using existing and well-maintained exclosures, we were able to measure community change at long temporal scales (mean exclosure age is 32 years) and at reasonably large spatial scales (mean exclosure size is 1000 m<sup>2</sup>). By conducting our work within a reserve that has been free from cattle grazing for over 70 years, we focused specifically on the role of native consumers in oak persistence and the invasion of oak savanna communities by nonnative plants. In the context of this replicated large-scale experimental consumer manipulation, we asked the following questions. (1) Do vertebrate consumers affect recruitment of

native oaks? (2) Do vertebrate consumers have different effects on cover and richness of native and exotic species?

In our study system, all exotic plant species were annual grasses and forbs, while native species were composed of annual and perennial grasses and forbs, shrubs, and trees. We examined responses to consumers across all groups and then compared native and exotic annuals directly to isolate whether any differences between native and exotic species were primarily a function of provenance (native vs. exotic) or life history (annual vs. perennial).

## METHODS

This study was conducted in 2005–2006 on Hastings Natural History Reservation, a 932-ha University of California Natural Reserve lying 40 km southwest of Carmel, California, USA (36°23'17" N, 121°32'60" W). Elevation ranges from 467–953 m and average precipitation is 530 mm/yr. Agricultural grazing has been absent from Hastings since 1937 and the guild of large carnivorous vertebrates is largely intact with two felid (*Felis concolor*, mountain lion and *Lynx rufus*, bobcat) and two canid (*Canis latrans*, coyote and *Urocyon cinereoargenteus*, gray fox) species as top predators. The most important exotic consumers are feral pigs, *Sus scrofa*.

### Consumer manipulations

We conducted our research at 10 sites scattered across the grasslands and oak woodland communities of the reserve. Each site has an exclosure established between 1965 and 1992 (mean age = 32 years) by a variety of researchers for different projects (see Table 1). The exclosures range in size from 16 to 5000 m<sup>2</sup> (mean area = 1021 m<sup>2</sup>) and are bordered with various fencing materials. At each site, we demarked an adjacent area of equal size and geometry as the exclosure to serve as a paired control to quantify the effects of the exclosure. The control and exclosure plots were sampled in an identical fashion. These exclosures sorted vertebrate

TABLE 2. Number (mean  $\pm$  SE) of individual small mammals captured inside and outside of exclosures (three fence types), 5–10 June 2006.

Species	Complete vertebrate food web (outside controls)	Large-vertebrate exclosures	Fossorial-vertebrate exclosures	Climbing- and fossorial-vertebrate exclosures
<i>Reithrodontomys megalotis</i>	0.9 $\pm$ 0.2	0.6 $\pm$ 0.3	5.0 $\pm$ 0.5	0.7 $\pm$ 0.4
<i>Chaetodipus californicus</i>	0	0	0	1.3 $\pm$ 0.4
<i>Microtus californicus</i>	0.2 $\pm$ 0.2	0	0	0
<i>Peromyscus boylii</i>	0.4 $\pm$ 0.2	0	0	0
<i>Neotoma fuscipes</i>	0	1.0 $\pm$ 0.3	0	0

consumers into four distinct groups, each containing granivores and herbivores capable of directly affecting oak and grassland dynamics.

1) Complete vertebrate food web ( $N = 10$  plots). These areas represent comparison plots for exclosures and are composed of the full suite of terrestrial vertebrate consumers.

2) Large vertebrate exclosures ( $N = 5$  plots). These plots have barbed wire to at least 2 m and wire mesh (15 cm) fencing to at least 1.25 m. These exclosures prohibit access by large consumers such as *Sus scrofa* (European wild boar), and *Odocoileus hemionus* (mule deer) that are known to have potentially strong effects on oak recruitment and survival (Bartolome et al. 2002, Sweitzer and Vuren 2002).

3) Fossorial vertebrate exclosures ( $N = 2$  plots). These plots consist of 1 cm of fine mesh buried into the ground and at least 1 m above the ground. These exclosures prohibit access by fossorial and semi-fossorial vertebrates such as voles (*Microtus californicus*), rabbits (*Sylvilagus audubonii*), and gophers (*Thomomys bottae*), but do not exclude small climbing vertebrates or large vertebrate consumers. Pocket gophers have been shown to be one of the major sources of acorn predation in some areas of California (Borchert et al. 1989).

4) Climbing and fossorial vertebrate exclosures ( $N = 3$  plots). These plots have barbed wire to at least 2 m, wire mesh (15 cm) to at least 1.25 m, fine mesh (1 cm) extending 1 m above and various distances below the ground and metal flashing from 1–1.5 m. These exclosures prohibit access by all vertebrate herbivores (fossorial and large vertebrates), and many vertebrate omnivores (e.g., brush mice, *Peromyscus boylii* and woodrats, *Neotoma fuscipes*), and terrestrial vertebrate predators, including snakes (e.g., western rattlesnake, *Crotalus viridis* and gopher snake, *Pituophis catenifer*). Only arthropods, birds, and particularly agile consumers such as harvest mice (*Reithrodontomys megalotis*) have access to these areas. These exclosures allow us to focus exclusively on the role of arthropods and small omnivorous rodents, which are known to have important short-term effects on oak recruitment (e.g., Swiecki et al. 1991), but whose long-term effects are unknown.

#### Oak and herbaceous plant community

We quantified oak seedling and sapling density, understory community composition, community bio-

mass (estimated by light interception), and the abundance of small mammal consumers inside and outside of each exclosure. We note here that four of these plots were planted with oaks or other species as a part of the original experiment. We excluded from our plot-scale analyses all species that were planted by the original researchers.

All plant data were collected during the period of peak vegetation biomass, between the months of May and June of 2005. Vegetation cover was recorded using cover classes (0–5%, 6–25%, 26–50%, 51–75%, 76–95%, 96–100%) in 50  $\times$  20 cm quadrats. Cover was estimated separately for all species, so total cover can be greater than 100%. Cover data from quadrats were collected along transects evenly placed throughout the exclosure; the number of quadrats sampled was scaled to the size of the exclosure with one quadrat for every 1 m of linear dimension (i.e., the square root of the area in m<sup>2</sup>). Overstory tree canopy cover for trees with stems > 5 cm dbh was estimated for each quadrat, and total canopy cover of the exclosure was estimated as the proportion of quadrats with overstory canopy greater than 0. Oak seedlings and saplings (trees with stems < 5 m dbh) in each quadrat were tallied.

We measured several other environmental covariates, as well. Photosynthetically active radiation (PAR), a metric of light limitation for seedlings, was measured in each quadrat at 1.5 m (above the understory vegetation) and at ground level. We collected three 10 cm soil cores from the inside and outside of each exclosure to quantify nine soil characteristics, including several macro- and micronutrients, pH, and texture (A and L Western Agricultural Laboratories, Modesto, California, USA). Finally, because animal-generated disturbance also can be important for invasion, we recorded the percent cover of gopher and pig disturbances in each vegetation quadrat.

#### Exclosure efficacy and small-mammal community composition

To determine the efficacy of exclosures for manipulating smaller mammals, we trapped small, non-fossorial mammal consumers at each study site (Table 2). We focused on non-fossorial rodents, because the presence of fossorial vertebrate consumers (i.e., gophers) can be accurately determined by the presence of fresh gopher mounds. No mounds were found inside of fences

TABLE 3. Effects of consumers and resources (light and soil nutrients) on richness of native and exotic understory plants.

Parameter	Exotic annuals		Native annuals		Native perennials		Native shrubs	
	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>
Intercept	3.678	<0.001	2.395	<0.001	-0.728	0.009	-0.343	0.253
Enclosure area (m <sup>2</sup> )					0.294	<0.001	0.229	0.001
Enclosure age (yr)							-0.023	0.030
Presence of consumers (yes or no)	1.544	0.003			-0.319	0.043		
PC3 (Low P vs. high clay and CEC)					0.147	0.033		

*Notes:* Blank cells are terms dropped from regression model during backward selection. There were no significant interactions between consumer treatment and the three resource gradient variables (PC1, PC2, PC3). Oak canopy (%), presence of oak canopy (yes or no), PC1 (high sand vs. low nutrient), and PC2 (low light and pH vs. high P) were included in the original model but were not significant in any of the reduced models. CEC is cation exchange capacity.

designed to exclude fossorial rodents during the study. At each site, we placed six large live traps (Tomahawk Traps, Tomahawk, Wisconsin, USA) and 12 small live traps (H. B. Sherman Company, Tallahassee, Florida, USA). Use of two trap types allowed us to reliably capture larger vertebrates (e.g., squirrels and rabbits) as well as smaller vertebrates (e.g., voles and mice). At each site, half of the traps were placed within the enclosure and half were placed in the paired plot outside of the enclosure. All live traps were placed in the field on 5 June 2006, baited, and locked open to allow animals to acclimate to their presence. Small live traps were activated at dusk on 6 June 2006 and checked every morning. Large live traps were opened from dawn until approximately 10:00 hours each day. Upon capture, animals were identified to species, and their age, reproductive status, and body mass were determined. They were quickly released at the site of capture. After checking, all traps were closed to prevent captures during the day when animals might become unduly stressed. This process was repeated daily until 10 June, when traps were checked and removed. Our single five-day trapping session was not intended to provide an exhaustive sampling of the rodent community in each treatment. Rather, these data provide valuable insight into the effects of the various enclosure types on the small-mammal community (see Table 2).

#### *Statistical analysis*

All statistical analyses were conducted in R (Version 2.3.1; R Foundation for Statistical Computing, Vienna, Austria). We analyzed community responses to consumers using mixed-effects regression models in which experimental blocks (composed of an adjacent enclosed and open plot) were treated as random effects. We included treatment (consumer presence or absence) as a fixed effect. We included three covariates in all analyses: enclosure area, age of enclosure, percent canopy cover of oaks, and a binary variable distinguishing sites with no oak canopy whatsoever. Our initial plotting of the data indicated that in many cases oak canopy effects were discontinuous and were best modeled as a binary step function.

Consumer effects on communities can be mediated by resource gradients (Hillebrand et al. 2007). To examine

the role of resources in mediating consumer effects we incorporated data from nine soil variables and light availability (PAR) in the regression models. We reduced these 10 variables using principal components analysis, because the high degree of colinearity in the raw variables tended to make the models unstable and difficult to interpret. We also included the interactions between consumer presence and each of the resource variables. We removed nonsignificant terms from the model using backwards selection following Crawley (2005).

We did not have sufficient degrees of freedom to include the different types of enclosures, covariates, and interactions in a single model (Table 3). We conducted separate analyses using a model without any interactions that included variables distinguishing plots that excluded only large vertebrates (burrowers and climbers were present), excluded burrowers (climbers were present), and excluded large, burrowing, and climbing vertebrates (only small and flying vertebrates present) as well as the environmental covariates (Table 3). We discuss the few significant differences among enclosure types, but do not present the full model here.

## RESULTS

### *Environmental gradients*

Our sample areas covered a wide range of resource gradients. Light (PAR) at ground level ranged from 26% to 81% of ambient. Soils varied more than fivefold in phosphorous, nitrate, potassium, and organic matter. The physical soil environment was also variable with concentrations of sand (50–88%), silt (6–26%), and clay (6–28%) varying widely across the sites. Canopy cover of adult oaks ranged from 0% to 62%.

Resource pools were highly collinear, such that 76% of the original variance across the 10 variables at our 20 sites (10 enclosure pairs) was accounted for by three orthogonal PCA (principal components analysis) axes based on correlational distance (Table 4). The first axis (PC1) was positively correlated with sandy low-fertility soils having low levels of organic matter, nitrate, phosphorous, potassium, and cations. The second axis (PC2) was positively correlated with acidic, phosphorous-rich, nitrogen-limited soils that were also light

TABLE 4. Results of light and soil principal components analysis (PCA) based on correlation matrix of 10 original variables.

Variables	PC1	PC2	PC3
Proportion of variance	0.56	0.16	0.14
Loadings of original variables			
Light transmission (proportion PAR)	0.183	<b>-0.505</b>	-0.068
Organic matter (%)	-0.375	-0.195	-0.152
Nitrate (ppm)	-0.283	-0.359	-0.390
Phosphorous (ppm)	-0.206	<b>0.402</b>	<b>-0.540</b>
Potassium (ppm)	-0.346	0.178	-0.079
Sand (%)	<b>0.402</b>	-0.126	-0.179
Silt (%)	-0.373	0.310	-0.081
Clay (%)	-0.340	-0.106	<b>0.425</b>
pH	-0.241	<b>-0.439</b>	-0.358
Cation exchange capacity (mmol/100 g)	-0.331	-0.264	<b>0.418</b>

Note: Variables with absolute loadings greater than 0.4 are shown in bold.

limited (i.e., high aboveground biomass). The third axis (PC3) was positively correlated with phosphorous-poor, clayey soils with high cation exchange capacity.

Oak canopy cover was unrelated to any of the environmental variables; however there was a bias with larger exclosures being located in areas with more closed canopies (Table 5, Fig. 1). There were no differences in oak canopy cover or any of the resource variables (light and soils characteristics) between the two main consumer treatments (control vs. enclosed).

#### *Vertebrate consumers do not affect recruitment of native oaks*

Across all 10 pairs of exclosures ( $N = 20$ ), we found seedlings of two species of oak (mean density in stems/ha): *Quercus douglassii* (6705) and *Q. lobata* (434). The mean density of *Q. agrifolia*, *Q. douglassii*, and *Q. lobata* at these sites was 128, 729, and 1667 saplings/ha, respectively. While mean recruitment was quite high, about half of the 20 plots had no recruits while the remainder had very high densities, suggesting that some sites were inherently unsuitable. The seedlings and saplings of all oak species exhibited a similar pattern, and in the following we describe the aggregate response of the saplings and seedlings. Oak recruitment was unaffected by any of the consumer treatments, but was positively correlated with the presence of adult oaks (Table 5; Fig. 1).

#### *Vertebrate consumers have different effects on native and exotic understory species*

Overall, the presence of consumers led to a 41% higher exotic species richness and a 31% higher exotic species cover (Tables 3 and 6, Fig. 2). In our analyses that included exclosure type as a factor, the increase in exotic richness was independent of exclosure type, while the increase in exotic cover was primarily driven by the presence of burrowing vertebrates ( $P = 0.021$ ). While this effect was associated with the exclusion of

burrowing vertebrates, the higher cover and richness of exotics did not arise from a direct effect of soil disturbance; the effect of consumer exclusion on exotic cover remains significant in regression models that include the cover of gopher and pig disturbance. Finally, exotic annual cover was 40% lower under the existing oak canopies, but exotic cover and richness were not explained by gradients in light or soil resources.

Consumers reduced the richness of native herbaceous perennial species by 33% (Table 3, Fig. 2). This decline in native perennial richness was driven by the presence of climbing vertebrates in our regression that included exclosure type as a variable ( $P = 0.022$ ). As a group, native annuals and woody species were unaffected by consumers. Native shrub cover was higher in areas with more oak canopy cover. Overall native cover and richness were unaffected by gradients in light or soil resources; however native perennial richness was higher in clayey soils with low phosphorous.

Exclusion of vertebrates led to strong species-specific responses that were generally concordant with the group-level responses. For example the five species that declined most strongly when exposed to consumers were all natives (*Lupinus nanus*, *Lotus purshianus*, *Clarkia unguiculata*, *Nassella pulchra*, and *Madia elegans*), while the four species that increased most in the presence of consumers were all exotics (*Erodium botrys*, *Bromus hordeaceus*, *Aira caryophylla*, and *Bomus diandrus*). The 10 most abundant plant species in the control plots outside of the exclosures, in order of abundance, were *Erodium botrys* (17.6%), *Avena fatua* (14.2%), *Bromus hordeaceus* (13.2%), *Bomus diandrus* (8.4%), *Trifolium hirtum* (8.3%), *Torilis nodosa* (4.3%), *Galium aparine* (3.8%), *Nassella pulchra* (3.5%), *Hypochaeris glabra* (3.5%), and *Clarkia purpurea* (3.4%). The 10 most abundant species inside the exclosures in order of abundance were *Avena fatua* (14.6%), *Bromus hordeaceus* (11.3%), *Trifolium hirtum* (8.2%), *Bomus diandrus* (7.2%), *Erodium botrys* (5.2%), *Galium aparine* (4.6%), *Lupinus nanus* (4.4%), *Nassella pulchra* (4.3%), *Clarkia*

TABLE 5. Effects of consumers and resources (light and soil nutrients) on canopy cover by adult oaks (percent) and recruitment of oak seedlings and saplings (stems/m<sup>2</sup>).

Parameter	Oak recruits		Oak canopy	
	Estimate	P	Estimate	P
Intercept	-0.003	0.985	-0.299	0.020
Exclosure area (m <sup>2</sup> )			0.082	0.002
Oak canopy (%)			NA	NA
Presence oak canopy (T/F)	1.272	0.001	NA	NA
Presence of consumers (T/F)			NA	NA

Notes: Blank cells are terms dropped from regression model during backward selection. There were no significant interactions between consumer treatment and the three resource gradient variables (PC1, PC2, PC3). Exclosure age (yr), PC1 (high sand vs. low nutrient), PC2 (low light and pH vs. high P), and PC3 (low P vs. high clay and CEC) were included in the original model but were not significant in any of the reduced models.

*purpurea* (4.1%), and *Torilis nodosa* (3.6%). Mean percent cover across all plot is given in parentheses.

#### *Efficacy of mammal exclosures*

Small-mammal sampling suggested that exclosures were working as intended (see Table 2). No small mammals were found inside the fences designed to exclude them, except a single individual pocket mouse, *Chaetodipus californicus*, that was captured inside a climbing vertebrate exclosure. Three harvest mice, *Reithrodontomys megalotis*, were also found within climbing vertebrate exclosures, but these exclosures were not intended to exclude them, and harvest mice were ubiquitous. In total, the number of individuals captured was (proportion of total captures in parentheses): 15 harvest mice (0.65), three brush mice, *Peromyscus boylii* (0.13), two woodrats, *Neotoma fuscipes* (0.09), two voles, *Microtus californicus* (0.09), and one pocket mouse (0.04).

Pig disturbance was quite rare in our study areas, though it is common elsewhere at Hastings Reserve. We found pig disturbances outside of three of our exclosures (cover  $1.3\% \pm 3.49\%$  [mean  $\pm$  SE],  $n = 10$ ). No pig disturbances were found inside of any exclosures. Gopher disturbances were more common than pig disturbances, with a cover of  $9.63\% \pm 3.49\%$  ( $n = 10$ ) outside exclosures and  $2.58\% \pm 1.4\%$  ( $n = 10$ ) inside exclosures. No pocket gopher disturbances were found in sampled areas enclosed by buried fences.

#### DISCUSSION

Our long-term study yielded two key findings. First, consumer communities dominated by native consumers can have transformative effects on native grasslands, reducing the richness of native perennials and increasing the cover and richness of exotic annuals. A largely native vertebrate food web increased the cover and richness of exotic plant species, concurrently suppressing the richness of native perennial species. Second, oaks can play an important role in facilitating the diversity of native forbs and grasses. While our specific results may not apply to other oak savanna systems, the long-term nature of this study provides a clear demonstration of the importance of native consumers and positive interactions in mediating biological invasions.

While we know that consumers can have dramatic effects on species richness, composition, and ecosystem function (Huntly 1991, Hillebrand et al. 2007), our findings suggest that native consumers may facilitate invasion, in contrast to a recent meta-analysis suggesting that native consumers reduce biological invasions (Parker et al. 2006). Our results are concordant with several recent studies demonstrating that native consumers may facilitate invasions in California grasslands (Schiffman 1994, Seabloom and Richards 2003, Orrock et al. 2008a, b). This finding is significant because invasions mediated by native consumers pose a fundamentally different problem from the perspective of

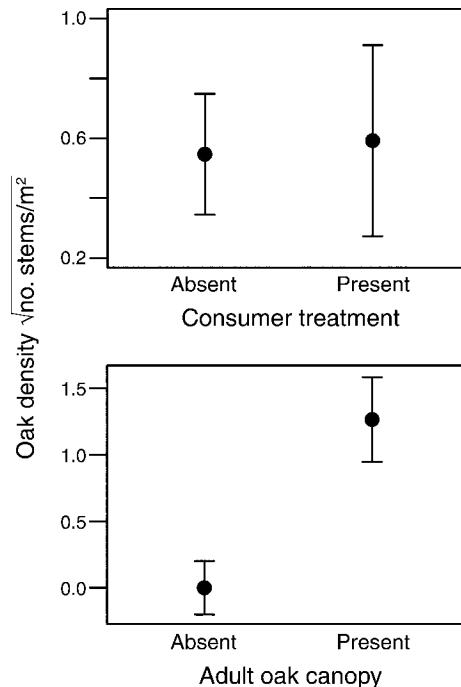


FIG. 1. Effect of consumer exclusion and adult oak canopy on density of oak seedlings and saplings.

conservation and restoration, i.e., removal of exotic plants and exotic consumers alone may be insufficient to reverse invasions. The long-term perspective of this study demonstrates that consumer-mediated shifts in plant communities are likely to represent alternative stable states that are stable over long periods of time and unlikely to change unless consumers are manipulated (Seabloom and Richards 2003, Suding et al. 2004).

The positive link between native consumers and invasion was not driven by a bias in life history types between the native and exotic floras, although California's exotic flora is heavily biased towards annual life history and annual grasses in particular (Seabloom et al. 2006). While all exotic species were annuals, native annual responses to consumers and the environment were more concordant with longer-lived natives than with exotic annuals; as a group, native annuals were unaffected by consumers and increased under oak canopies (Fig. 2). This may arise in part from long-term evolutionary history. Many of the exotic annuals that dominate California's grasslands originate in the Mediterranean region and have had a long history of adapting to heavy grazing in agricultural landscapes (Diamond 1999, D'Antonio et al. 2007). In addition, species-specific responses to consumers were most strongly negative for several natives and most strongly positive for a suite of exotics. Recent work has highlighted the role of consumers in promoting seed limitation in species such as lupines and several of the native grasses that also declined in our study (Maron and Vila 2001, Orrock et al. 2008a), thus our results

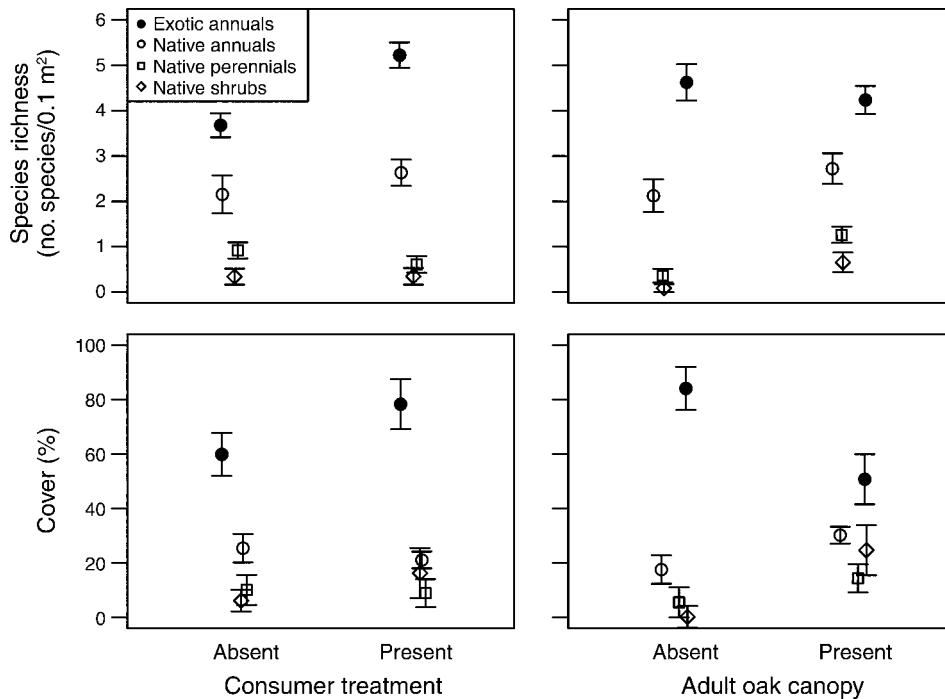


FIG. 2. Effect of consumer exclusion and adult oak canopy on the richness and cover of native and exotic annuals and native perennials and shrubs.

suggest that consumer-driven seed limitation may disproportionately depress some important native species, facilitating invasion.

Although animal-generated disturbance can promote invasion (Seabloom et al. 2005, Harrison et al. 2006, Buckley et al. 2007), our evidence did not support this consumer effect as the driver of invasion in our study. The only fairly common exotic vertebrate affected by the exclosures at our study site is the feral pig. While feral pigs can have massive effects on plant communities (Cushman 2007), our results do not support the presence of feral pigs as drivers of invasion in our study plots; pig disturbance was not found in any exclosure and was uncommon even in our control plots, though pig impacts can be substantial in other locations on the Reserve. Although exotic cover increased most strongly in the presence of buried fences that controlled access by burrowing vertebrates, we also found that the elevated

cover and richness of exotics did not arise from the direct effect of soil disturbance. In addition, the decline in native perennials was associated with presence of fences excluding climbing vertebrates rather than large or fossorial vertebrates (e.g., feral pigs, deer, or gophers).

While native consumers increased invasion, adult oaks provided refugia with enhanced recruitment of native oaks and lower cover of exotic species. The lack of recruitment in areas with no adult oaks is unlikely to have been due to seed supply alone, as three of the areas with no canopy cover had oaks planted in them in the past (Muick 1991), none of which were found alive in our surveys. It is well established that adult oaks and shrubs can act as nurse plants to enhance oak seedling and sapling survival (Callaway and D'Antonio 1991, Muick 1991, Callaway 1992, 1995) and that oaks can act as arbiters of competition among exotic grasses (Cal-

TABLE 6. Effects of consumers, soils, and system productivity (biomass) on cover of understory plants.

Parameter	Exotic annuals		Native annuals		Native perennials		Native shrubs	
	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>	Estimate	<i>P</i>
Intercept	0.726	<0.001	0.233	<0.001	0.095	0.105	-0.006	0.910
Oak canopy (%)							0.717	0.004
Presence oak canopy (T/F)	-0.255	0.011						
Presence of consumers (T/F)	0.159	0.011						

Notes: Blank cells are terms dropped from regression model during backward selection. There were no significant interactions between consumer treatment and the three resource gradient variables (PC1, PC2, PC3). Exclosure area (m<sup>2</sup>), exclosure age (yr), PC1 (high sand vs. low nutrient), PC2 (low light and pH vs. high P), and PC3 (low P vs. high clay and CEC) were included in the original model but were not significant in any of the reduced models.

laway et al. 1991, Rice and Nagy 2000). This study demonstrates that the keystone effects of oaks in the grasslands of California extend to facilitating the richness of native herbaceous perennials. These findings suggest that conservation and restoration of oaks is likely to have benefits for grasslands as a whole. Moreover, these benefits are realized regardless of whether or not consumers have access, i.e., increasing the recruitment of oaks may provide an effective way to promote restoration of native grassland communities without the need for manipulating consumer pressure. Although our results are encouraging, other authors have noted that the effect of oaks on herbaceous plant communities is likely to vary with site productivity (Tyler et al. 2007), and oaks may provide areas where exotic plants proliferate (Tyler et al. 2007). However, because these studies are restricted to relatively short time scales, it remains unclear whether the facilitation of exotics by oaks is a transient phenomenon; our data suggest that, over longer time scales, oaks may have beneficial impacts on native grassland communities (Fig. 2).

In general, we found fairly high levels of oak recruitment. There has been a great deal of research examining oak regeneration problems in California (Tyler et al. 2006, Zavaleta et al. 2007), however some large-scale surveys indicate that there is ample recruitment at least on federally owned forest lands (Gaman and Casey 2002). In our surveys, we found more than 100 saplings per hectare of even the least common of the three oak species (*Q. agrifolia*). The discrepancy between the perceived problems with oak recruitment and these data could arise from two sources. First, this work has been conducted on a reserve that has not been grazed for 70 years. Statewide surveys indicate that oak recruitment is higher on reserves (Zavaleta et al. 2007). Second, the perceived lack of saplings could arise from differences in sampling techniques. We intensively searched small areas for saplings that are not detectable in aerial surveys and are easy to overlook in an understory comprised of small trees and shrubs. At least at our site, it appears that three of the oak species are replacing themselves inside and outside of exclosures. Our results arise from a uniquely long-term and large-scale experiment, a critical perspective for understanding dynamics of long-lived species such as oaks (Tyler et al. 2006). In particular, recruitment patterns of these long-lived species are likely to become apparent only after several decades. The strength of the results presented here is increased by the concordant response of the saplings and seedlings, indicating that our results are not based on a single recruitment event.

The results of our long-term experiment suggest that both native consumers and native oaks are key groups in determining the composition of California grassland communities. These groups not only control the balance of native and exotic herbaceous plants, but also the recruitment dynamics of oaks, themselves. Native consumers and adult oaks strongly control community

composition; however both groups also are subject to contemporary forces of change. For example, loss of large carnivores (i.e., "mesopredator release") is likely to affect consumer guilds, with largely unknown consequences for grassland systems (Crooks and Soule 1999). Similarly, an emergent disease, sudden oak death, has killed over a million native oak and tanoak trees and is found in over 14 coastal California counties (Rizzo et al. 2002, Rizzo and Garbelotto 2003). Finally, California's oaks and native consumers may continue to experience a regionally changing climate (Hayhoe et al. 2004), which also is likely to dramatically change population dynamics for both groups, even in protected areas (Kueppers et al. 2005). Our work provides a first step for predicting the trajectories of oak recruitment and grassland invasion, but has implications for interactions among species groups in other grassland ecosystems, as well. Finally, our work highlights the importance of native consumers in facilitating biological invasion. This is a largely unstudied relationship that warrants significant future attention.

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